THE

TONGUE AND GUSTATORY ORGANS

OF

MEPHITIS MEPHITICA.

BY

FREDERICK TUCKERMAN, M.D.Harv.,

AMHERST, MASS., U.S.A.

Reprinted from the 'Quarterly Journal of Microscopical Science,' August, 1887.

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With Plate XI.

It is now twenty years since Christian Lovén (26)[1] and Gustav Schwalbe (37) discovered and described, independently of each other, the peripheral end-organs of the nerves of taste in the tongue of Mammalia. Subsequent investigators have studied the distribution and minute anatomy of these organs in many animals, and in all essential points they confirm the results reached by Lovén and Schwalbe.

Before passing to the consideration of my own observations I will briefly review what is known regarding the position and structure of the taste organs of Vertebrates.

Bellini, nearly two hundred years ago, considered the papillæ of the tongue to be organs of taste.

In 1846, Waller (50) investigated the epithelium of the fungiform papillæ of the frog, and also studied the cilia and ciliary movement. In 1847, he (51) concluded, from the experiments of Longet, that the glosso-pharyngeus was the nerve of taste for the base of the tongue and the lingual for the tip and anterior third. He succeeded in tracing nerves into the base of the fungiform papillæ of the frog, and into the papillary elevations on the tongue of the toad. He believed the fungiform or "neurovascular" papillæ to be the chief

[1] These figures refer to the bibliography at the end of the paper.

organs of taste in the frog. The soft palate has also, he says, the power of taste. The conical papillæ he considered tactile organs. In 1849 he (54) redescribed these organs, and also speaks of the gustatory nerves terminating in the fungiform papillæ on the dorsum of the tongue, and of a gustatory area situated at the summit of each papilla.

In 1851 Leydig (23) described in the external skin of fresh-water fishes certain beaker- or flask-shaped bodies, which he was disposed to regard as organs of a tactile nature. In 1857, he showed (24) that the epithelium covering the end surfaces of the fungiform papillæ differs from the rest of the epithelium. Later investigators, with the exception of Fixen, have confirmed this.

In 1863, F. E. Schulze (34) redescribed the beaker-shaped bodies of fishes, and considered them organs of taste. He found them in greatest number where the fibres of the glosso-pharyngeal nerve are most thickly distributed, i. e. in the mucous membrane of the palate, upon the gums and tongue rudiment, on the inner side of the gill arches, and upon the lips. In structure he found them to agree, in most respects, with the organs of taste of the frog. The beakers he described as composed of two kinds of cells, viz. Sinneszellen and Stützzellen, or sensory and supporting cells; the former having a peripheral and central process. In 1867, he stated (35) that the peripheral extremity of the taste-cell bears a fine hair-like process as in mammals. In 1870, Schulze (36) described, in the papillæ of the mouth of a larval amphibian (Pelobates fuscus), bodies resembling in structure the beaker-shaped organs of fishes, which he considered taste organs.

In 1872, Todaro (44) described, in the papillæ covering the rudimentary tongue of Trygon pastinaca, a number of club-shaped bodies connected with the ultimate ramifications of the glosso-pharyngeus nerve, which he regarded as organs of taste and analogous to those of mammals. At the base of the gustatory organ the nerve loses its sheath, and the fibrillæ of the axis cylinder separate and join the central processes of the taste-cells.

Jourdan quite recently (18) has pointed out on the gills and in the buccal cavity of the malarmat, cup-shaped bodies composed of central and peripheral cells, which, in structure and situation, differ completely from the organs of touch, and which he regards as taste-bulbs.

In 1858, Billroth (4) described the peculiar epithelium of the taste papillæ of the frog, and believed that certain of its cells were continuous with nerve-fibres. The smaller papillæ he thought were unprovided with nerves.

Hoyer (16) differed from Billroth in supposing that the nerves terminate bluntly beneath the epithelium.

In 1861, Key (19) described in the frog two kinds of cells at the summit of the fungiform papilla,—epithelial cells and taste-cells. He speaks of the penetration of the axis cylinder alone into the papilla, and its division into fibres which enter the taste-cells at its summit. The "nerve-cushion" of Engelmann he considered an enormous enlargement of the neurilemma and called it the "nerve-shell."

Hartmann (10) thought that the nerves ended in plexuses beneath the epithelial cells of the fungiform papillæ.

Beale (2), Engelmann (7), and Maddox (29) supported Key, believing in a structural continuity between the cells at the top of the papilla and the nerve-fibres in its axis. The former, however, did not consider the cells to be of epithelial origin.

In 1868, Engelmann (8) described, in the fungiform papilla of the frog, numerous dichotomous subdivisions of the nerve-fibres, which form a close network and spread out in the lower half of the "nerve-cushion" in nearly a horizontal direction. The upper part of the papilla consists of a solid disc composed of non-nucleated connective tissue, which he calls the "nerve-cushion," and upon which rests the taste disc. The latter is composed of three distinct kinds of cells, viz. cup-shaped, cylinder, and forked. The two former he considered were epithelial cells only. The forked cells he regarded as the end-organs of the gustatory nerve, probably being directly continuous with pale nerve-fibres, which in their chemical reaction they resemble. Engelmann says that the nerve-fibres just

before entering the "nerve-cushion" lose their medullary substance and neurilemma.

In 1869, Beale (3) redescribed the epithelium of the papillæ of the frog, and reiterated his disbelief in the existence of structural continuity between nerve-fibres and epithelial cells. He figured fine nerve-fibres ramifying in the connective tissue of the simple papillæ, and connected with them oval-shaped masses of germinal matter or nuclei, formerly supposed to be connective tissue. He believed in a connection between the cells upon the summit of the fungiform papilla and the nerve-fibres in its axis, but did not consider the former epithelial in structure. He figured a nervous plexus containing nuclei at the top of the papilla, the fibres of which are derived from the nerves in its axis, and from which fine fibres may be traced into the special organ composed of "epithelial-like" cells. He found that the bundle of nerve-fibres distributed to a papilla always divides into two, which pursue opposite directions; this division taking place either at the base of the papilla or at some distance from it.

In 1869, Maddox (29) regarded the fungiform papillæ as the chief organs of taste in the frog, and described the nerves of taste as possessing terminal organs consisting of nerve matter.

In 1867, Szabadföldy (43) described the nerves of taste as terminating in mammals in pear-shaped bodies lying in the mucous membrane of the tongue. Two years later Letzerich (22) called attention to a peculiar way in which these nerves end in the papillæ of the cat, ox, and weazel. In neither case have the results reached by these observers been verified.

In 1867, Lovén (27) described the taste-bulbs (Geschmackszwiebeln) or taste-buds (Geschmacksknospen) of mammals. He studied them in the circumvallate papillæ of the cat, rabbit, pig, sheep, calf, dog, horse, and man, and found them to consist of central and peripheral cells. The outer or cover-cells, for support and protection; the inner or taste-cells, bearing a central and peripheral process, the former being continuous with a nerve-fibril, the latter terminating in a delicate hair-like extremity which projects a short distance beyond the opening

of the bulb. He says that in man and the calf the gustatory nerve-fibres lose their medullary sheath in the outer layer of the mucous membrane, the axis cylinder being prolonged into the bulb, where it divides into terminal branches which are distributed to the taste-cells. In the calf the peripheral process of the taste-cell carries no hair at its extremity. Lovén found taste-bulbs and cells on the upper surface of the fungiform papillæ of the calf, rat, and rabbit, the small ones containing a single specimen only. He also detected in the rat and rabbit a few taste-bulbs in the outer wall of the trench encircling the circumvallate papilla.

In 1867, Schwalbe (37) published the preliminary report of his investigation of the "Schmeckbechers" in the papillæ of the sheep, ox, horse, dog, cat, and rabbit. His detailed account (38) of the taste-goblets of these animals, including also those of the deer, pig, guinea-pig, hare, and man, appeared the following year. His description of their location and structure agrees essentially with that given by Lovén. He found taste-bulbs in man and the dog on the outer wall of the trench surrounding the circumvallate papilla, and in the fungiform papillæ and lateral organ of taste of the pig. He notes in man and the sheep two kinds of taste-cells, namely, staff-cells (Stabzellen) and needle-cells (Stiftchenzellen). He found in the sheep at the apex of the bulb, after treatment with per-osmic acid, a circle of fine short hairs or cilia, which appeared to spring from the end of the cover-cells. In the sheep also, at the base of the circumvallate papilla, is a richly-developed nervous plexus. He speaks of the small branches of the glosso-pharyngeus being provided with ganglia, especially where the nerve divides at the base of the papilla.

Engelmann (9) found bulbs in the fungiform papillæ of the mouse and cat, and described them in the lateral organs of taste (papillæ foliatæ) of the rabbit and hare. He says that usually the central process of the taste-cell divides, at a short distance from the nucleus, into two branches. He speaks of groups of ganglion-cells in the branches of the glosso-pharyngeus ramifying beneath the taste-ridges of rodents, and points

out the resemblance in physical characteristics and chemical reaction of nerve-fibrils with the central processes of the taste-cells.

In 1869, v. Wyss (56) described the taste-bulbs in the papilla foliata of the rabbit and hare, and called attention to the analogous organs of man. In 1870, (57) he studied them in the circumvallate and fungiform papillæ of many mammals, including the hedgehog and squirrel; but failed to find them in the fungiform papillæ of man.

Krause (20) observed taste-bulbs in the fungiform and foliate papillæ of man, and v. Ajtai (1) described them in the papilla foliata of man and other mammals.

Hönigschmied (12 and 13) has shown the distribution of the taste-bulbs in the circumvallate and foliate papillæ of various mammals, and, in some, has found them occurring on the summit of the papilla, though these were usually smaller than those on the sides. By means of chloride of gold, Hönigschmied traced the nerve-fibrils directly into the taste-cells in the fungiform papilla of the cat, the cover-cells not being stained, while the taste-cells were. Vintschgau and Hönigschmied (47 and 49) found in the rabbit that, after section of the glosso-pharyngeus nerve, the taste-bulbs degenerate, while the cover-cells become changed into epithelial cells in a few months. Ranvier (32) repeated this experiment, and has met with a similar result.

Sertoli (41) states that he has traced nerve-fibrils directly into the taste-bulbs in the papilla foliata of the horse. In the fungiform papillæ of the same animal he says that the nerves terminate in an intra-epithelial plexus of fine non-medullated nerve-fibrils.

Hoffmann (14) found taste-bulbs on the summit of the fungiform and circumvallate papillæ of man, and also in some papillæ of the soft palate and upper part of the uvula. He failed to find in the epiglottis what he considered genuine taste-bulbs.

In 1868, Verson (45 and 46) described in the second fourth of the posterior surface of the epiglottis of man, certain "bud-like structures," which resembled mammalian taste-bulbs.

Krause (21) observed them on the dorsal surface of the epiglottis of the sheep and rabbit. Schofield (33) has described them in the lower half of the posterior surface of the epiglottis of the dog and cat, arranged in horizontal and vertical rows. He says that with each "goblet" is associated the duct of a mucous gland. In 1873, v. Ebner (6) pointed out that the serous glands always occur in the parts of the tongue that contain taste organs, and their ducts open into the furrows lined by the taste-bulbs. Davis (5) studied the bulb-shaped organs in the epiglottis of the cat, dog, calf, pig, rabbit, and man, and found them on the upper and lower parts of the posterior surface of that organ. In the dog he found them on the inner side of the arytenoid cartilages, on the aryepiglottic folds, and in the epithelium of the true vocal cords. He regarded them as terminal organs of the glosso-pharyngeal nerve. Simanowsky (42) has also seen them on the true vocal cords of man and the dog. In the vocal cord of the dog and rabbit he figures the nerve-fibres as terminating in pencil-shaped extremities. Hönigschmied has observed bulbs on the epiglottis of the deer and calf.

Poulton (30) has described, in a highly interesting and suggestive manner, the taste-bulbs of Perameles nasuta. The circumvallate papillæ, he says, are highly developed in shape and structure, and in the abundance of nervous and glandular tissue which they possess ; but the terminal organs he considers of a low type. Within the papillary body is a large ganglion, which divides into branches running towards the sides of the papilla containing taste-bulbs. The nerve-fibres are chiefly non-medullated, but possess a distinct sheath of Schwann. He found near the top of a single fungiform papilla two bulbs of a low order. Poulton (31) found in the posterior region of the tongue of Ornithorhynchus paradoxus two pairs of gustatory areas. The anterior pair lie below the surface in a furrow, the floor of which is invaginated upwards into a ridge, which carries the taste-bulbs. The ridges of the posterior pair reach the surface. In both regions the bulbs are situated on the sides and upper surface of the ridges, and the ducts of

serous glands open into the spaces around them. The centre of the ridge is nearly filled by non-medullated nerve-fibres, which radiate outwards to end in the bulbs. The bulbs are developed at the ends of long papillary processes. Nerve-fibres can be followed into the bulbs where they pass between the cells in various places. Poulton suggests "that the primitive type of bulb was papillary in position and subepithelial in structure, and has gradually given way to a bulb that was interpapillary and epithelial."

Among recent observers who have studied the taste organs of mammals, especially with regard to development, are Lustig (28) and Hermann (11). The former has described the development of the taste-bulbs of man and the rabbit, and the latter has investigated the papillæ, circumvallatæ, and foliatæ of the fœtal and newborn rabbit. In the papilla circumvallata of the latter Hermann found taste-bulbs on the summit. Boulart and Pilliet (58) have, within a short time, examined the tongues of a number of mammals, with special reference to the presence or absence of the papillæ foliatæ.

Holl (15) has lately studied the taste organs of Salamandra maculata. Goblet-shaped sense organs, or end-bulbs have been described by Leydig (25) in the skin and mouth of various snakes, and Wiedersheim (55) says that they are present in the lizard and blindworm on the inner sides of the upper and lower jaws. Ihlder (17) has described the ending of nerve-fibres in the tongue of birds. He traced them into oval, concentric, club-shaped bodies, like those seen by Krause and Kölliker in the lingual papillæ of mammals.

The Tongue of Mephitis mephitica.

The tongue about to be described was taken from quite a young animal, and the following method was adopted in preparing it for histological examination. As soon as removed from the body it was placed in a mixture of five parts Müller's fluid and one part alcohol. After remaining in this mixture for ten days it was washed for thirty-six hours in running water, and then transferred to strong alcohol, where the har-

dening was completed. Subsequently portions of the organ were embedded in celloidin in the usual manner. My efforts to obtain sections stained with chloride of gold were not successful.

General Description of the Tongue.—The organ is 44 mm. long, 19 mm. wide, and 9 mm. in thickness. It is perfectly free for 15 mm. from the frænum, or a trifle more than one third of its length. Its length is therefore a little more than twice its width, which is quite uniform from the base to near the apex. Here it becomes thinner and somewhat elliptical in form. The upper surface is slightly convex posteriorly, and more or less flattened near the anterior extremity. There is a very slight raphé running forwards from the middle third of the tongue to its junction with the anterior third; here it takes the form of a shallow groove, which disappears just before reaching the tip. There is also a well-defined mesial groove at the posterior part of the dorsum, commencing midway between the two circumvallate papillæ, and running backwards for 10 mm. In the anterior third, beginning a little back from the apex, and reaching to the lateral margin, are four or five transverse ridges with corresponding depressions curving backwards, which give to this part of the tongue a corrugated appearance.

The upper surface, including the lateral margins in front of and lying between the circumvallate papillæ, is covered with tactile and mechanical papillæ, the points of which are directed backwards. These become gradually smaller as they approach the anterior extremity. The region of the tongue lying behind the gustatory area has projecting from its surface large cone-shaped papillæ, the apices of which are directed backwards and inwards. These increase in size, but decrease in number, as they recede towards the posterior limits of the organ.

Papillæ of the fungiform type are scattered quite uniformly over the dorsum and upon the sides of the middle third of the tongue, but terminate posteriorly in front of the area of the circumvallate papillæ. The average distance between them in this region is about 0·5 mm. They are very sparingly dis-

tributed to the anterior third, and are much smaller than those of the middle portion.

On each lateral half of the tongue is situated, near the anterior margin of the posterior third of the papillary surface, a large circumvallate papilla. These two papillæ lie in the same plane, and are 6 mm. apart. The left one is a little the larger of the pair. They are elliptical in form, and are placed at an oblique angle to the long axis of the tongue, with their anterior extremity directed outwards. Each papilla is encircled by a deep and rather wide trench, in which it is quite movable. Around the trench, and also forming part of its wall, are large conical-shaped papillæ. The larger of the two circumvallate papillæ measures, at its summit, 2 mm. in its long diameter, and 1·4 mm. in its short. The upper surfaces of both present an uneven or ridged appearance. No papilla foliata was found.

The under surface of the tongue is perfectly smooth except at the borders and tip, at which points are distributed numerous small tactile or mechanical papillæ. Anteriorly it is marked by a deep median groove, commencing at the frænum and running towards the apex. This becomes, however, rapidly superficial, and disappears altogether about 9·5 mm. from the tip.

The Circumvallate Papillæ.—These papillæ are distinctly lobate posteriorly; their upper and lateral contours are necessarily, therefore, somewhat uneven and irregular. Still, in some sections, I found the sides comparatively symmetrical. The diameter of the papilla at its base is always less than at the summit. In many sections the sides are vertical, or slightly oblique for about half their length, and then bend inwards and downwards.

The relation of the trench to the shape of the papilla is peculiar and, so far as I am aware, quite unusual (see figs. 2 and 3). Posteriorly, it is wide and deep, and passes directly beneath the papilla, thus giving it (the papilla), for about half its diameter, a free under surface.

Anteriorly and externally the trench becomes narrower

(though this is not constant) and more shallow. This pedunculated arrangement of the base of the papilla accounts for its free mobility, first noticed in the superficial examination. In some sections the trench is so extremely narrow that the surfaces of the opposing walls are almost contiguous. The width of the trench is usually greater in its upper portion, becoming, in most cases, gradually narrower as it curves downwards and inwards. The outer wall reaches nearly to the level of the upper surface of the papilla. Serous glands are present in the body of the papilla, but both mucous and serous glands (the latter being the more numerous) are very abundant in this region of the tongue. The ducts of the serous glands open into the trench, either at its sides or where it passes beneath the papilla. They are very plentiful. In one small horizontal section I counted twelve separate (?) ducts. Towards its upper part the papilla carries many secondary papillæ, the depressions between them being filled by epithelium. The nerves are mainly non-medullated. They form a network in the upper part of the papillary axis, from which branches radiate outward towards the lateral margins, terminating, apparently, at or near the bases of the taste-bulbs.

The taste-bulbs are very numerous in the circumvallate papillæ. They are distributed along the sides in a zone of ten or twelve tiers or rows, but are most thickly placed at the under surface of the papilla facing the bottom of the trench. The bulbs in this situation, although protected to a remarkable degree, are often smaller and less fully developed than elsewhere. I counted here, in one horizontal section, a group of forty-five on a surface 0·3 mm. square. The estimate of the number of these structures cannot be very exact. In one quarter of a horizontal section, made at the lower third of the papilla, I counted fifty-five bulbs. If we allow 200 in each tier, and allow ten tiers, we shall have 2000 bulbs for each papilla, or 4000 for the two. Bulbs are also present in the epithelium bordering the mid-trench (fig. 3) between the two large divisions of the papilla. In one section I met with them (fig. 3) on the free upper surface. I likewise found them in

the lower half of the outer wall of the trench. In some vertical sections they are arranged along the sides and lower surface in several rows.

The bulbs are quite irregular in size, and exhibit some variation in shape (fig. 5 shows the structure of the bulbs magnified 240 diameters. Their average length is about 0·06 mm.). The neck is very short and narrow, and only in a single bulb did I observe hair-like processes protruding through the pore. The nuclei of the peripheral cells stain quite deeply in hæmatoxylin. The outer layer of epithelium, at the point of its perforation by the bulbs, stains a uniform yellow in picro-carmine. I did not succeed in identifying gustatory as distinct from covering cells, though by teasing I was enabled to dislodge several bulbs from their position in the epithelium, and, in one case, to isolate a bulb with a nerve-fibril attached to or entering its base.

The Fungiform Papillæ.—These papillæ offer nothing very unusual in their general appearance. In shape they resemble the human type. A variation from the normal, however, is seen in their distribution, they being more numerous and larger over the middle of the dorsal surface than elsewhere.

In a few cases I found isolated taste-bulbs in the epithelium at the upper part of the papilla. The best specimen is represented by fig. 6. This papilla contains two bulbs, but they are neither of them of a high order. They are arranged obliquely near the summit, with their apices directed outwards and upwards, and measure about 0·05 mm. in length, and 0·032 mm. in breadth. In none of my sections do they appear to reach the surface of the epithelium.

Non-medullated nerve-fibres are quite abundant in the upper part of the body of the papilla, and nerve-fibrils can be seen running directly beneath the epithelium containing the taste-bulbs. Beyond this point I was unable to trace them. A few collections of ganglion-like cells are scattered along the course of the nerves. In some of the papillæ the nerve-fibres terminate in end-bulbs, as already pointed out by Krause and

Kölliker. Neither serous nor mucous glands were observed near the fungiform papillæ.

The tactile and mechanical papillæ are very numerous, covering the upper surface of the tongue from the base to the apex. They are largest at the posterior part of the dorsum (behind the gustatory structures), and diminish in size, but increase in number and density, as they approach the anterior extremity. One that I measured, from the posterior part of the dorsum, was 1·8 mm. in height. About the middle of the tongue I counted twenty-five on a square millimetre of surface. Here they are 0·25 mm. in height. They present considerable variation in shape. Anteriorly they are flattened, or slightly convex on the top, with their sides vertical, forming either a right angle with the upper surface, or having their upper edges slightly rounded. Occasionally the sides are prolonged upwards for a short distance, terminating in spiniform processes. Interspersed among these papillæ, but chiefly confined to the gustatory area and posterior surface, are a few cone-shaped ones, the points of which are directed backwards and inwards. Each papilla is usually seated upon two papillary upgrowths of the mucosa. The free surface is covered with a thick layer of cornified epithelium, which, in the cone-shaped, papillæ, presents an imbricated arrangement. In their internal structure these papillæ do not differ materially from ordinary conical papillæ.

It is probable that the cone-shaped papillæ of the anterior and middle dorsal surface of the tongue are mechanical rather than tactile in function.

On the posterior surface of the epiglottis, near the line of union of the first and second fourth, I noticed in the stratified pavement epithelium a few isolated bulb-like structures. I did not, however, meet with them below this point. In the same region, on the right side, I found the bulb-like structure shown in figure 7. It will be seen at once that it is entirely subepithelial in position and structure. It occupies a cavity of the mucosa, with its apex resting against the base of the deep layer of columnar cells of the epithelium. Its length is

about 0·045 mm., and its greatest transverse diameter about 0·025 mm.

I examined a very large number of sections of the soft palate and uvula, but did not succeed in finding any bulb-like structures.

To sum up briefly in conclusion, there are situated at the posterior part of the tongue of Mephitis two large circumvallate papillæ. Upon superficial examination the most striking features are their size, the ridged appearance of their upper surface, and their rather unusual shape. Under the microscope each papilla is seen to be divided posteriorly into two unequal lobes or divisions, and to have in the same region a free under surface, the trench passing directly beneath its base, thus affording great protection to the bulbs occurring here. Anteriorly the papilla is connected with the tongue by a pedicel-like attachment.

The taste-bulbs of the circumvallate papillæ are very numerous, especially in the epithelium of the under surface, and offer considerable irregularity in shape, size, and distribution. A few bulbs occur in the epithelium of the upper surface of the papillæ, and in that of the outer wall of the trench. In a single instance I observed a bulb with a nerve-fibril attached to its base. Glands of the serous and mucous types are very abundant, but the former are chiefly limited to the gustatory area of the tongue. Serous glands are also met with in the papillary body itself.

A few fungiform papillæ possess isolated bulbs lying in the epithelium at their summit, and they also occur in the upper part of the posterior surface of the epiglottis; but in both these regions they are primitive in character and position.

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EXPLANATION OF PLATE XI,

Illustrating Mr. Frederick Tuckerman's paper on "The Tongue and Gustatory Organs of Mephitis mephitica."

FIG. 1.—Vertical section through the right circumvallate papilla. *S. P.* Secondary papillæ. *t.* The trench. *r.* Section through the ridge which surrounds the trench. *t. b.* The taste-bulbs arranged in tiers. *gl. d.* The ducts of the serous glands, opening into the bottom of the trench. *m. m.* Mucous membrane. (× 20 times.)

FIG. 2.—Vertical section through the same circumvallate papilla. *S. P.* Secondary papillæ. *t.* The trench. *r.* Ridge. *C. P.* Conical papilla, somewhat depressed. *t'.* The trench passing beneath the papilla, showing the arrangement of the taste-bulbs in the epithelium of the under surface. *gl. d.* The ducts of the serous glands. (× 24 times.)

FIG. 3.—Vertical section through the posterior part of the same papilla. *t.* The trench. *t. b'.* Taste-bulbs in the epithelium of the upper surface. *m. t.* The mid-trench, partly separating the papilla into two divisions. *gl. d.* Ducts of the serous glands. (× 20 times.)

FIG. 4.—Vertical section through the anterior part of the same papilla. *t. b.* Taste-bulbs, divided at right angles to their long axis. *gl. d.* Ducts of the serous glands. (× 30 times.)

FIG. 5.—Vertical section through the base of the same papilla, showing the bottom of the trench and the six lowest tiers of taste-bulbs. *t.* The trench. *t. b.* Taste-bulb. *g. p.* Gustatory pore. *s. e.* Stratified epithelium. *o. l.* Outer layer of stratified epithelium. *gl. d.* The ducts of the serous glands. *m. m.* Mucous membrane. (× 240 times.)

FIG. 6.—Vertical section through a fungiform papilla, from the group in front of the circumvallate papillæ. *t. b.* Taste-bulbs. *p. p.* Papillary processes. *s. e.* Stratified epithelium. (× 220 times.)

FIG. 7.—Transverse vertical section through the upper part of the posterior surface of the epiglottis. *f. s.* Free surface of the stratified pavement of epithelium. *d. l.* Deep layer of columnar cells of the epithelium. *b. l. s.* Bulb-like structure lying in the mucosa, with its apex touching the base of the cells of the deep layer of epithelium. *m. m.* Mucous membrane. (× 240 times.)

Fig. 1.

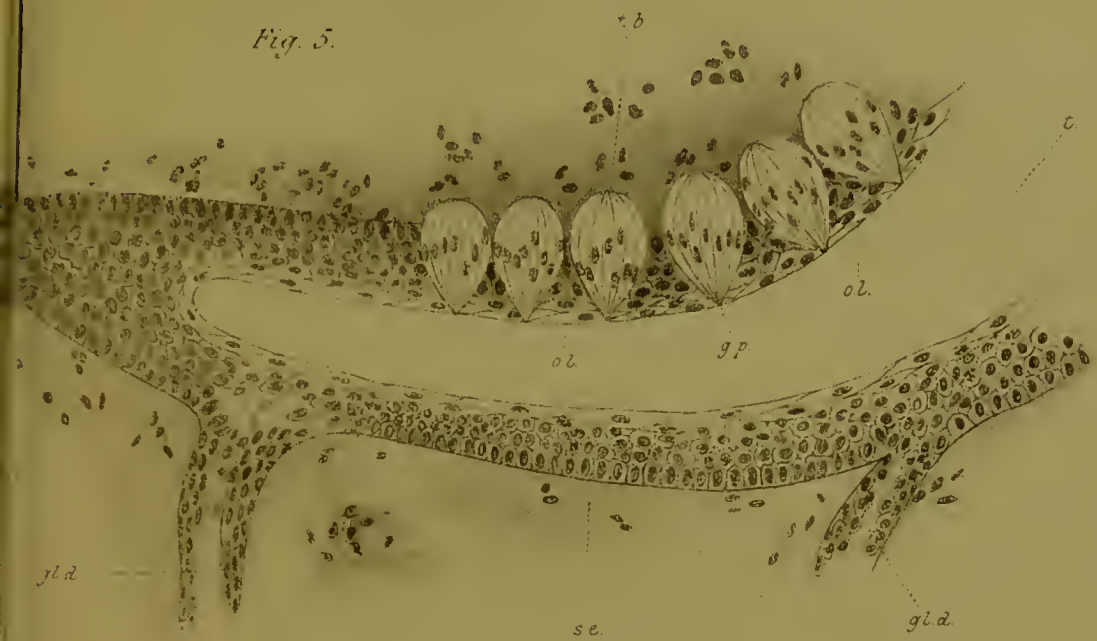
Fig. 2.

Fig. 3.

Fig. 4.

K. I. Hah. del.

Fig. 5.



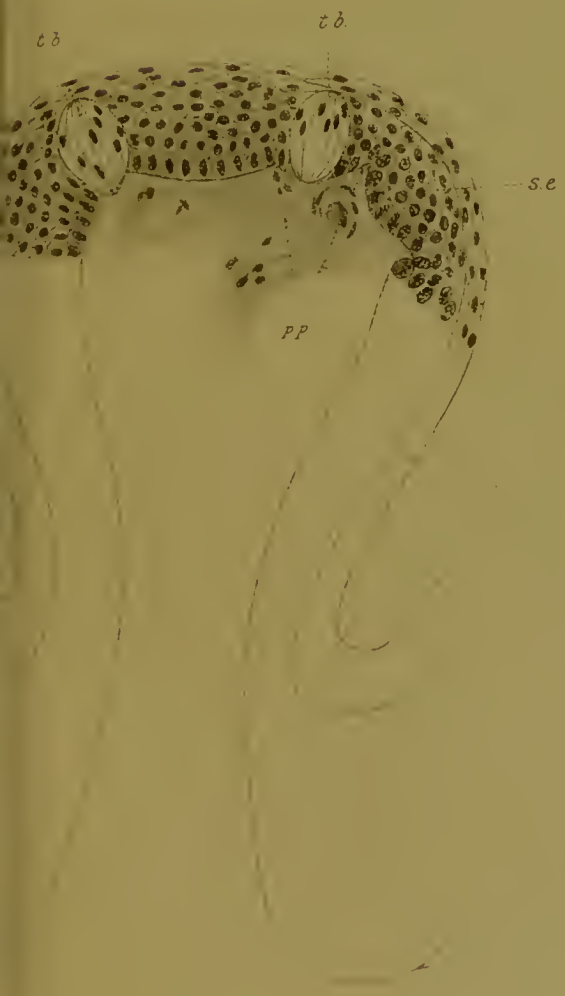
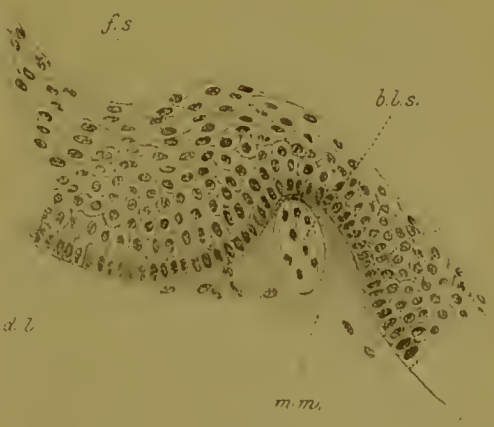


Fig. 7.



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